RESPONSES OF COASTAL WETLANDS TO RISING SEA LEVEL

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Abstract. Salt marsh ecosystems are maintained by the dominant macrophytes that regulate the elevation of their habitat within a narrow portion of the intertidal zone by accumulating organic matter and trapping inorganic sediment. The long-term stability of these ecosystems is explained by interactions among sea level, land elevation, primary production, and sediment accretion that regulate the elevation of the sediment surface toward an equilibrium with mean sea level. We show here in a salt marsh that this equilibrium is adjusted upward by increased production of the salt marsh macrophyte *Spartina alterniflora* and downward by an increasing rate of relative sea-level rise (RSLR). Adjustments in marsh surface elevation are slow in comparison to interannual anomalies and long-period cycles of sea level, and this lag in sediment elevation results in significant variation in annual primary productivity. We describe a theoretical model that predicts that the system will be stable against changes in relative mean sea level when surface elevation is greater than what is optimal for primary production. When surface elevation is less than optimal, the system will be unstable. The model predicts that there is an optimal rate of RSLR at which the equilibrium elevation and depth of tidal flooding will be optimal for plant growth. However, the optimal rate of RSLR also represents an upper limit because at higher rates of RSLR the plant community cannot sustain an elevation that is within its range of tolerance. For estuaries with high sediment loading, such as those on the southeast coast of the United States, the limiting rate of RSLR was predicted to be at most 1.2 cm/yr, which is 3.5 times greater than the current, long-term rate of RSLR.

Key words: coastal wetlands; optimal elevation, model; salt marsh; sea-level rise; sediment accretion; sedimentation; Spartina.

INTRODUCTION

As sea level rises, the long-term sustainability of salt marsh and mangrove ecosystems is dependent upon the dominant macrophytes that maintain the elevation of their respective habitats within a relatively narrow portion of the intertidal zone. The relative elevation of the sediment surface determines the duration and frequency that these habitats are submerged by the tides, which is critically important to a wide variety of organisms, including the macrophytes. These dominant salt marsh and mangrove macrophytes are said to be foundation species (Pennings and Bertness 2001) because of their modification of the physical environment, their influence on species interactions and resource availability, and the subsequent effect they have on community structure (Bruno and Bertness 2001). Consequently, plant species of salt marshes and mangroves maintain a community of organisms that is quite distinct from the dwellers of the tidal mud flats that would dominate in their absence. However, the success of the macro-phytes in maintaining their environment depends on a number of factors including the rate of relative sea-level rise (land subsidence plus the eustatic change in sea level), sediment supply, and tide range (Stevenson et al. 1986, Reed 1995).

Salt marshes are known that have maintained an elevation in equilibrium with sea level for 4000 yr by the accumulation of mineral sediment and organic matter (Redfield 1965, 1972). Commonly, stable intertidal salt marshes occupy a broad, flat expanse of landscape often referred to as the marsh platform at an elevation within the intertidal zone that approximates that of the mean high tide (Krone 1985). The elevation of the platform relative to sea level determines total wetland area, inundation frequency and duration, and wetland productivity. Moreover, an absolute increase in the elevation of the marsh platform in response to rising sea level should cause a landward migration of the marsh (Gardner et al. 1992, Gardner and Porter 2001), and this may change total wetland area and consequently total production, depending on local geomorphology and anthropogenic barriers to migration. Therefore, understanding the processes that govern the elevation of coastal wetlands, such as sediment accretion, will enable us to predict their productivity and stability, par-
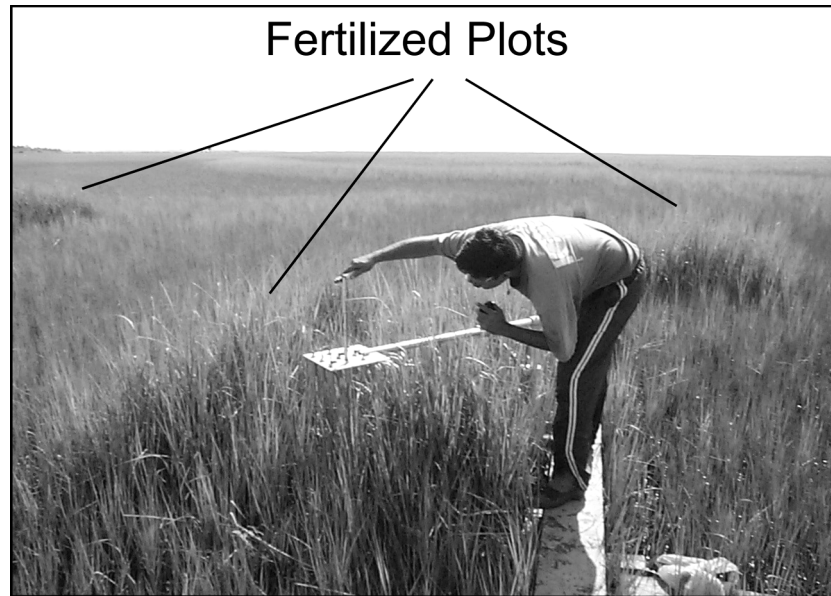
PLATE 1.   In this photo, the SET device is in place over a fertilized plot, the pins have been lowered to the sediment surface, and pin lengths above the plate are measured. Each SET site was bisected by a boardwalk with a fertilized plot along one side and a control plot on the opposite side.

ticularly in response to an acceleration in rate of relative sea-level rise (RSLR) brought on by global warming (Church et al. 2001). We report here results of a study of sediment accretion and its relationship to primary productivity and RSLR in North Inlet, a South Carolina salt marsh. We also present a general model that explains how the vegetation regulates the marsh elevation toward an equilibrium with mean sea level. Although the model was parameterized for North Inlet, its qualitative predictions are valid for any coastal wetland.

FIELD METHODS

Characteristics of the study site

The study was located on Goat Island within North Inlet estuary, which is also the location of a study of salt marsh primary production that has been in place since 1984 (Morris 2000). This marsh has transgressed over an old beach ridge such that 0.25–0.40 m of marsh sediment overlies well-sorted, tightly packed beach sands. North Inlet is a tidally dominated salt marsh estuary with a watershed area of ~75 km^2 and minimal freshwater input. North Inlet drains a 32 km^2 estuary of which ~82% is intertidal salt marsh, dominated by the grass *Spartina alterniflora* Loisel, and mud flat. 18% is open water. Our study was conducted on replicate ($n = 3$) control and nutrient-treated plots that were established in 1996 in a salt marsh dominated by a monoculture of short *S. alterniflora* in the middle of the marsh platform. The elevation of the site is close to that of the local mean high tide at ~60 cm above mean sea level. The nutrient-treated plots were fertilized with 30 and 15 mol·m^{-2}·yr^{-1} of N and P, respec-

tively, as NH_4NO_3 and P_2O_5 in six applications annually to the surface starting in June 1996.

Marsh surface elevation

Elevation change was measured with a Surface-Elevation Table (SET), which is a portable, mechanical leveling device designed to attach to a benchmark pipe driven into the ground (Boumans and Day 1993, Cahoon et al. 2002). Three permanent, replicate SET benchmark pipes were installed during May 1996, and first sampled on 19 June 1996. The pipes were driven 1 m below the sand/sediment contact with a sledgehammer in order to isolate the upper 1.0–1.5 m of the substrate where the biological processes of root growth and decomposition occur. Each benchmark pipe was established in the center of a paired plot, with a control plot on one side and a fertilized plot on the other (see Plate 1). The SET was attached to the benchmark pipe only during measurement and was then removed. Nine brass rods located in a plate at the end of an accurately leveled arm were lowered until they touched but did not penetrate the sediment surface. Elevation was recorded as the distance from the plate to the top of each rod. This procedure was repeated at six different positions around the benchmark pipe, three positions each in the control and fertilized plots of each pair. Change in elevation was determined by comparing repeated measures of monthly samples relative to the means of the first measurements. An assessment of the error of this technique was made on two different dates during 1998 when two operators (J. T. Morris and P. V. Sundareshwar) made independent measurements of surface elevations. The mean of the absolute value of differ-
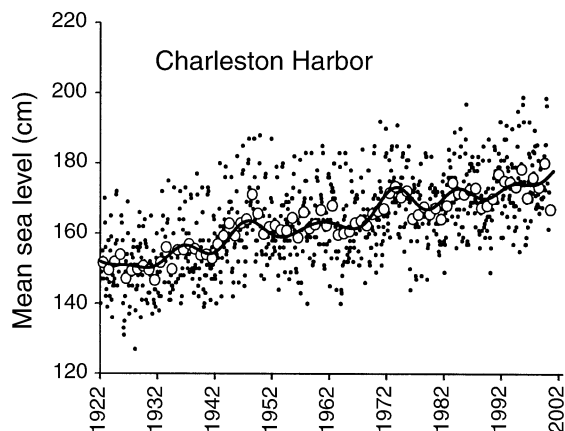
FIG. 1. Relative mean monthly (solid circles) and mean annual (open circles) sea level from Charleston Harbor, South Carolina, and the fit (solid line) of a Fourier analysis to the monthly data. Projected sea level over the next 25 yr (Fig. 6C) was based on this analysis.

ences in estimates of subplot elevations was 2.4 mm ($n = 36$), while at the plot and treatment level the error was ±1.3 mm ($n = 12$).

Vertical accretion was measured as the rate of accumulation of sediment above feldspar marker horizons laid upon the soil surface at the end of November 1997 according to the method of Cahoon and Turner (1989). Three months later small plugs of sediment, six to eight per treatment within each plot, were excised with a knife and the depth of sediment accumulated above the feldspar measured with a caliper. Significance of treatment effects was tested by Tukey's studentized range test ($\alpha = 0.05$).

Mean sea level

The rate of relative sea-level rise (RSLR) reported here is based on changes in mean water level relative to a NOS/NOAA tide gage in the harbor of Charleston, South Carolina, USA (Fig. 1). Fourier analysis of the time series of monthly mean sea-level data from this gage, based on hourly sea-level measurements from 1922 to 2000, yielded statistically significant peaks with periods equal to 113.8, 146.3, 170.7, and 341.3 mo. The Fourier coefficients were used to forecast relative mean sea level (see *Results and Discussion: Model development*) for the purpose of predicting changes in marsh surface elevation and productivity. These cycles are not astronomically forced, but are forced by climatic, hydrographic, or oceanographic variations. Thus, future projections are uncertain and meant only to illustrate the interaction between RSLR and marsh processes. Tidal harmonic analysis (Franco 1988) was also performed on the detrended ~79-yr hourly time series of sea-level data. The Charleston tide is semidiurnal with a form number of 0.20. The amplitudes and Greenwich epochs of the 13 major tidal constituents in order of decreasing period are Sa (8.4 cm, 179°),

Ssa (5.4 cm, 44°), O_1 (7.6 cm, 205°), K_1 (9.9 cm, 202°), $2N_2$ (2.1 cm, 345°), μ_2 (2.1 cm, 53°), N_2 (16.1 cm, 358°), ν_2 (3.5 cm, 357°), M_2 (74.3 cm, 13°), L_2 (3.7 cm, 6°), S_2 (12.9 cm, 40°), K_2 (3.3 cm, 40°), and M_4 (2.8 cm, 205°).

Primary production

Nondestructive measurements of aboveground production of *S. alterniflora* were begun at the Goat Island site in 1984. Net aboveground production was measured using a census technique, which was described in detail by Morris and Haskin (1990). At each site we selected six permanent plots. The dimensions of the plots were fixed so that each plot contained ~15 stems within a 1 dm² area. All stems in these plots were tagged with labeled plastic bands. Each month the lengths of all tagged stems were measured from the ground surface to the tip of the longest leaf. Newly emerged stems within each plot also were tagged monthly. Individual stem masses were estimated from stem heights using regression equations derived earlier from destructive harvests. This technique gives an estimate of monthly stem growth that is not biased by spatial variability.

RESULTS AND DISCUSSION

Field experiments

The productivity of coastal wetlands depends on numerous factors (Mendelssohn and Morris 2000), though the elevation of a site relative to mean sea level (MSL) is ultimately one of the most important. Relative MSL during the summer growing season affects productivity because it determines flood frequency and soil salinity (Morris 1995). Evapotranspiration can increase soil salinity to levels that reduce growth or are lethal (Phleger 1971, Haines and Dunn 1976, Bradley and Morris 1991, Morris 1995) when flooding occurs infrequently. Thus, sea-level rise and sedimentation rate interact to control productivity. For example, interannual changes in MSL on the order of 5–10 cm have a great effect on primary productivity of *Spartina alterniflora* (Morris et al. 1990, Morris 2000), which is the dominant macrophyte in salt marshes of the eastern and gulf coasts of North America. Within the intertidal range of *S. alterniflora*, primary production varies across the marsh surface and is characteristically greatest at the lowest elevations of its range (Pomeroy et al. 1981). At North Inlet, which is typical of transgressing, southeastern salt marshes, maximum production in the low marsh occurs at a depth between 40 cm and 60 cm below mean high tide (Fig. 2). At greater depths, growth of *S. alterniflora* is likely limited by hypoxia, and the marsh macrophyte community is replaced by unvegetated, tidal mud flats. Thus, there is an optimum marsh elevation for coastal wetland productivity, though apparently the optimum differs regionally as a function of tidal range and other factors (McKee and Patrick 1988).
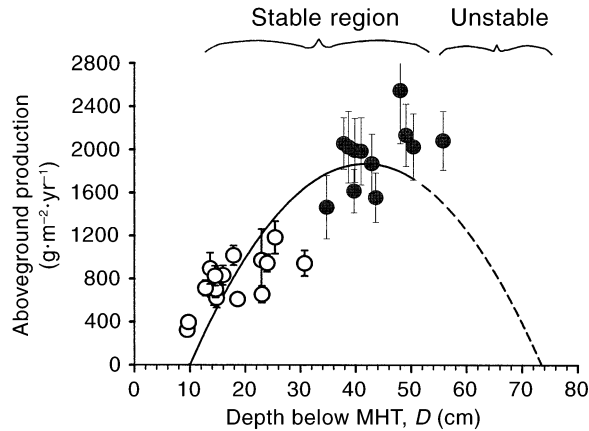
FIG. 2. Interannual variation in mean sea level resulted in this relationship between the observed productivity of the salt marsh macrophyte *Spartina alterniflora*, measured annually since 1984 (Morris 2000), and depth below mean high tide (MHT) of sites in the high (open circles) and low (solid circles) marsh. Depth below MHT was computed during the peak growing season months of July and August and is a highly significant predictor of productivity ($r^2 = 0.81$, $P < 0.0001$). Stable (solid line) or unstable (dashed line) combinations of equilibrium productivity, B, and depth, D, from Eqs. 2 and 4 are also shown for $a = 155$, $b = -1.855$, and $c = -1364$.

At North Inlet the majority of total marsh area is situated at an elevation that is higher than that which is optimal for primary production and that is dominated by a stunted form of *S. alterniflora* (Fig. 3). This constraint on productivity is an important factor in maintaining elevation because a rise in relative sea level brings about an increase in production and biomass density that will enhance sediment deposition by increasing the efficiency of sediment trapping (Gleason et al. 1979, Leonard and Luther 1995, Yang 1998). This positive effect of the plant community on sediment trapping was demonstrated experimentally at North Inlet (Fig. 4A).

In this study we examined the temporal response of the marsh surface to nutrient additions designed to stimulate primary production. Where primary production and biomass density were increased by fertilization, the rate of sediment accretion increased significantly above that of the controls (Fig. 4A). Plant biomass increased dramatically in fertilized plots begin-

ning in 1997, the second year of the experiment, and this corresponded to a rapid divergence in the elevations of fertilized and control plots (Fig. 4A). Mean aboveground dry matter production on fertilized plots increased to 3280 ± 300 g·m^{-2}·yr^{-1} (± 1 SE) from 780 ± 50 g·m^{-2}·yr^{-1} in control plots ($t_{15} = 5.8$, $P < 0.0001$). The balance between surface deposition and erosion apparently shifted abruptly in 1997 when plant biomass increased in fertilized plots. The corresponding, rapid divergence in elevations indicates that fertilized plots attained a new equilibrium elevation because of an increase in sediment trapping brought on by an increase in the density of plant biomass. This interpretation is supported by marker horizon data that showed fertilized and control plots accumulated 2.54 ± 0.94 and 0.99 ± 0.36 mm (± 1 SE) of sediment, respectively, in a 3-mo period following November 1997 ($F_{1,55} = 7.2$, $P = 0.01$) and supported by sediment cores that documented a decrease in sediment macroorganic matter in fertilized plots (Morris and Bradley 1999). Since 1997 the elevations of control and fertilized plots assumed significantly different ($F_{1,5214} = 75.4$, $P < 0.0001$) trajectories having slopes of 0.51 and 0.71 cm/yr, respectively, which was more than sufficient to compensate for the long-term rate of relative sea-level rise here of 0.34 cm/yr (Morris et al. 1990). Of this, 0.10–0.15 cm/yr is due to eustatic sea-level rise (Stewart et al. 1990).

Our data support the idea that homeostatic interactions among plants, relative sea level, and sediments maintain marsh elevation at North Inlet at a position within the intertidal zone that is supraoptimal for primary production. However, changes in the marsh surface are not as dynamic as changes in sea level (Fig. 4B). Mean sea level varies seasonally by ~30 cm (Kjerfve and McKellar 1980), and the marsh surface clearly does not respond with changes of this magnitude. But an annual cycle in marsh elevation was observed in fertilized plots (Fig. 4A) where a small, but statistically significant amplitude of 0.8 mm lagged the solar annual sea-level cycle (Fig. 4B) by one month. This annual cycle in marsh elevation may have been caused by seasonal changes in the relative magnitudes of deposition and erosion, belowground production and decay, or mean sea level.
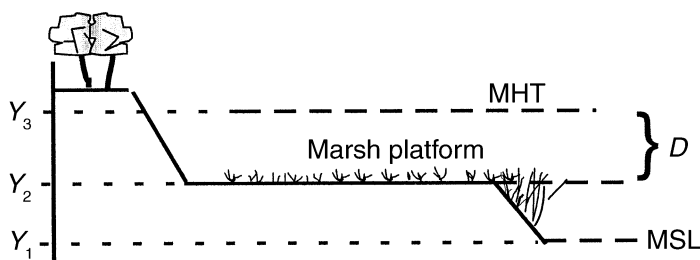

FIG. 3. Idealized geometric relationships among mean sea level (MSL) at elevation Y_1, mean high tide (MHT) at Y_3, and the equilibrium position Y_2 of the marsh platform at depth (D) relative to MHT.
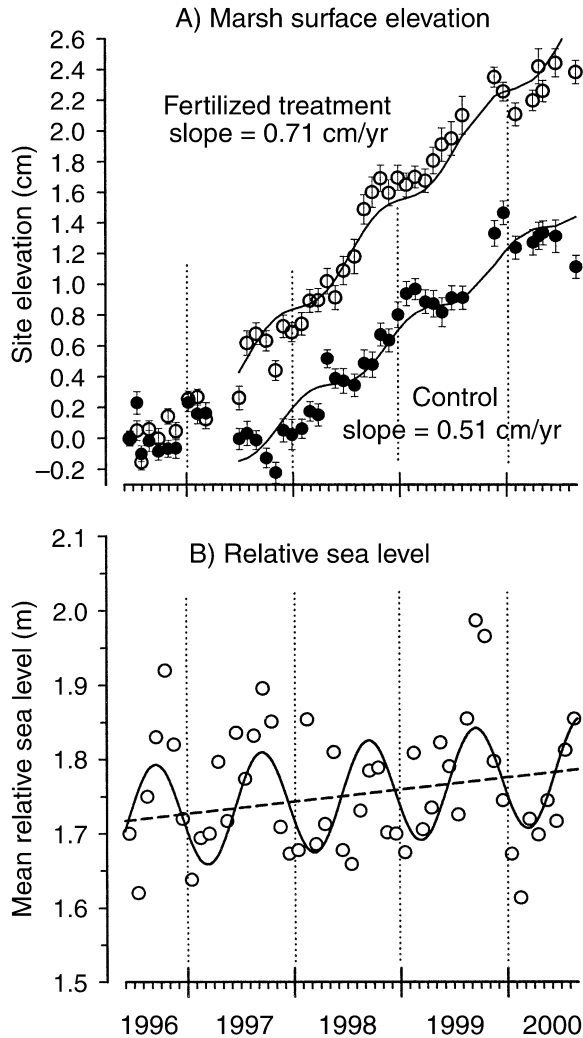
FIG. 4. (A) The relative elevation of permanent control (solid circles) and fertilized (open circles) salt marsh plots. Fertilization of these plots with N and P began in June 1996. Elevation is expressed relative to the elevation of the sites at the start of the experiment. The plots are located at the same high marsh site where long-term plant production has been monitored since 1984 (see Fig. 2). (B) Monthly mean sea level (open circles) from Charleston Harbor, South Carolina (NOAA data), and the solar annual cycle (solid line) around a trend line (dashed line) with slope = 1.6 cm/yr.

Model development

We developed a model of marsh sediment accretion by first stipulating that the elevation of the marsh platform is fixed at a position where erosional and depositional forces cancel each other. It is clear that sediment deposition must approach zero at elevations near that of the highest high tide, while a rise in relative sea level will increase flooding of the marsh, thereby increasing the opportunity for sediment deposition and reestablishing the elevation of the marsh relative to the new sea level (Pethick 1981, Krone 1985, French 1993). Thus, the net rate of change in the elevation of the marsh surface (dY_2/dt), also equivalent to the net rate of accretion (mineral and organic matter accumulation minus subsidence), is proportional to the depth (D) of the marsh surface below mean high tide (see Fig. 3): $dY_2/dt \propto D$. For simplicity we assume that this relationship is linear over the limited range of D that approximates the amplitude of the local tide and which effectively defines the boundary limits of the model.

The rate of change of elevation of the marsh platform is also a positive function of the standing density of plant biomass or aboveground production (B) as was demonstrated experimentally (Fig. 4A). For simplicity we assume that this relationship is linear: $dY_2/dt \propto q + kB$, where q and k are parameters that are proportional to the rate of sediment loading (q) and the efficiency of the vegetation (k) as a sediment trap. The k value would also account for positive contributions to elevation resulting from the accumulation of plant-derived organic matter (e.g., Bricker-Urso et al. 1989, Turner et al. 2000). The values of q and k are likely to vary locally and regionally as a function of sediment availability and tidal range (e.g., Stevenson et al. 1986). Combining these, the change in elevation of the marsh surface for depths (D) within the plant's growth range can be approximated by

$$dY_2/dt = (q + kB)D \qquad \text{for } D > 0. \qquad (1)$$

The coefficients q and k will vary somewhat with location within the marsh landscape because the rate of erosion and the opportunity for sediment deposition will vary with distance from tidal creeks, with bioturbation, plant community type, and other factors. These variations account for the gently sloping surface observed in real marsh landscapes and, while our idealized marsh landscape is a flat surface with zero slope (Fig. 3), Eq. 1 can be thought of as representing a family of equations with different coefficient values that apply to different zones within the marsh landscape. Generalities derived from the analytical solution to the model apply to any marsh locale, while quantitative predictions apply only to sites for which the model was fitted.

There exist both upper and lower limits of elevation for the productivity, B, of *S. alterniflora*. Thus, the variable B in Eq. 1 is a function of depth, D. This dependence of productivity on marsh elevation relative to mean sea level can be approximated by the following:

$$B = aD + bD^2 + c \qquad (2)$$

where a, b, and c are coefficients that determine the upper and lower depth limits, and magnitude of B. This equation is analytically tractable and satisfies the ecological principle that a plant's distribution will span a range of tolerance to an abiotic variable, like flooding depth, with an optimum somewhere in the middle of the range. Deviations from the perfect symmetry as-

sumed by this equation can affect the quantitative predictions of the model, but will not alter its generalities. Moreover, to emphasize the point that quantitative predictions are site specific, the values of the coefficients *a, b,* and *c* will differ regionally as a function of dominant species, tidal range, salinity, and climate.

For a marsh in equilibrium with mean sea level, the rate of change of marsh elevation (dY_2/dt) is equal to the long-term rate of change in sea level (dY_1/dt), which we assume is rising at a constant rate *r,*

$$dY_2/dt = dY_1/dt = r. \qquad (3)$$

Standing biomass or productivity affects elevation positively, and depth negatively, by increasing sedimentation (Eq. 1, Fig. 4A), while depths greater than or less than the optimum have negative effects on primary production (Eq. 2, Fig. 2). This reciprocal interaction between productivity (*B*) and depth below mean high tide (*D*) can be described analytically by substituting from Eqs. 1 and 2 and rearranging Eq. 3 to yield

$$kbD^3 + kaD^2 + (q + kc)D - r = 0. \qquad (4)$$

Eq. 4 was solved for different values of *r* to obtain *D,* and then Eq. 2 was solved for *B* (Fig. 5). Eq. 4 has two real roots that define a region of stability over a limited range of *r,* depending on the values of *a, b, c, k,* and *q.* Combinations of *B, D,* and *r* that represent one of the real roots to Eq. 4 correspond to equilibrium depths that are dynamically stable against changes in the rate of sea-level rise (denoted by solid lines in Fig. 5). In this region of largely suboptimal depths (*D*), the equilibrium marsh surface elevation will adjust upwards or downwards depending on changes in the local rate of sea-level rise. A second range of real roots (denoted by dashed lines in Fig. 5) corresponds to equilibria that are unstable against perturbations to sea-level rise and depths (relative to mean high tide) that are greater than optimal. Of course the model parameters (*a, b, c, k,* and *q*) can vary among and within estuaries. In general, marshes with relatively higher sediment loadings (*q*) and trapping efficiencies (*k*) can satisfy the equality in Eq. 4 and thus maintain stability against higher rates of relative sea-level rise (*r*).

The analytical solution of this model makes the simplifying assumption that dynamic variables such as the rate of sea-level rise are constant. In fact, mean sea level (MSL) displays a number of long-period cycles and climate-related noise, and therefore *r* is not constant. Consequently, the elevation of the marsh surface must constantly be adjusting. The temporal patterns of MSL and surface elevation (Fig. 4) demonstrate that the marsh surface and sediment accretion are much less dynamic than MSL on seasonal and interannual time scales. Thus, the marsh surface does not adjust quickly to interannual sea-level anomalies and must be in a constant state of disequilibrium with respect to mean sea level (Bricker-Urso et al. 1989). The response is probably complicated further by variations in sediment
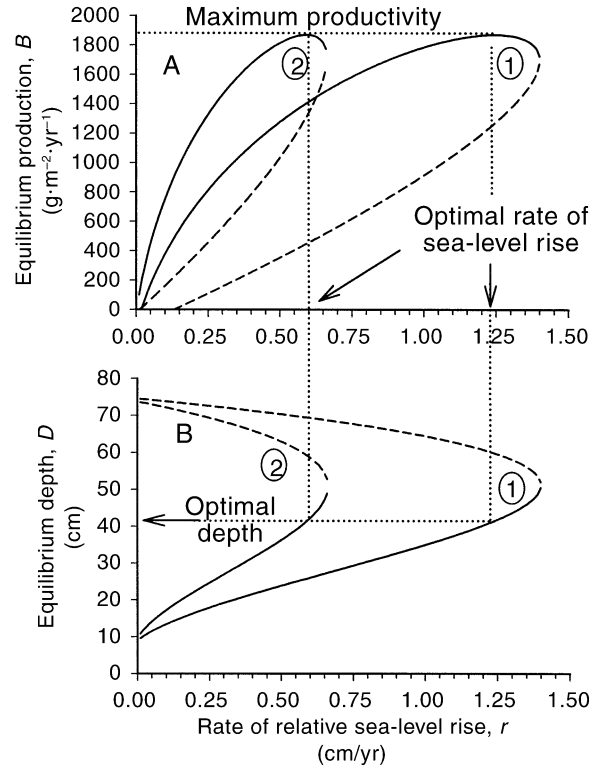

FIG. 5. Equilibrium combinations of (A) productivity and (B) depth below mean high tide (MHT) as functions of the rate of relative sea-level rise. Response curves were computed from Eq. 4 for estuaries characterized by (1) high ($q = 0.0018$, $k = 0.000015$) and (2) a hypothetically low ($q = 0.00018$, $k = 0.000015$) sediment loading. The optimal depth is the depth below MHT that results in maximum productivity. The solid portions of the curves (solid line) represent equilibrium conditions within a region of stability, where the system is stable against an increased rate of sea-level rise. The dashed line segments represent equilibrium conditions where the system is unstable against a change in the rate of sea-level rise.

supply brought on by changes in river discharge and by variations in primary production due to changes in nutrient loading and other factors.

A numerical simulation was run in order to examine the transient behavior of the model and to predict the effect of these sea-level anomalies on salt marsh productivity and sediment accretion (Fig. 6). Predicted annual production from year 1984 to 2025 was based on the empirical relationship of productivity to depth in high marsh sites (Fig. 2). Model coefficients *q* and *k* (Eq. 1), 0.0018 and 1.5×10^{-5}, respectively, were based on ^{210}Pb estimates of sediment accretion at North Inlet of 0.27 cm/yr (Vogel et al. 1996) and on differences in recent rates of sediment accretion between control and fertilized plots (Fig. 4A). An increase in RSLR to 0.4 cm/yr beginning in 1984 and then 1.64 cm/yr since 1996 accounts for a trend of increasing primary production that has prevailed since 1984 (Fig. 6A). Variability in summer MSL as great as ±20 cm/yr has also affected primary productivity (Morris 2000;
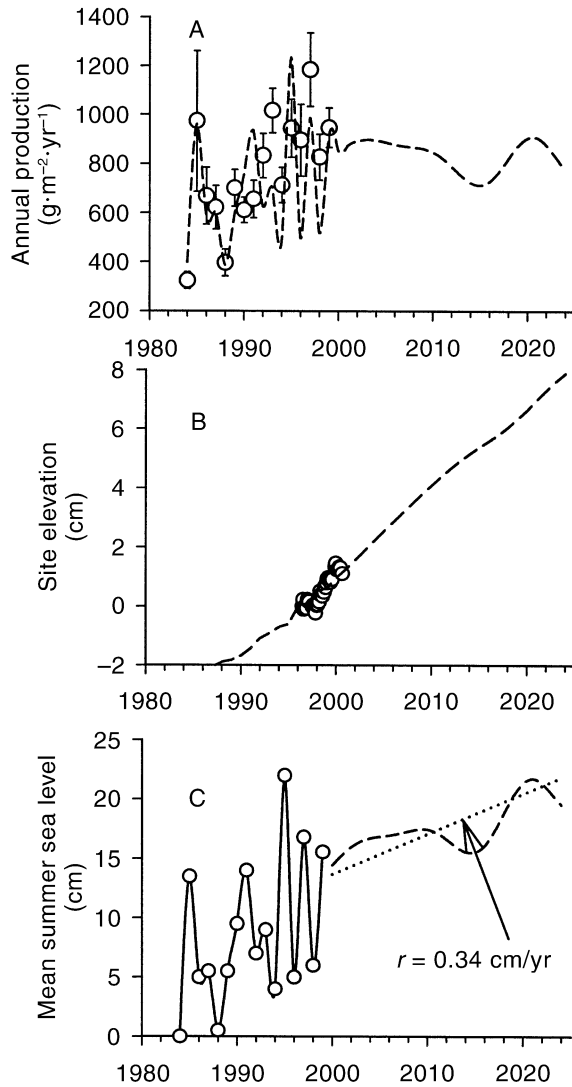
FIG. 6. (A) The predicted (dashed line) and observed (open circles) mean annual aboveground productivity of *Spartina alterniflora* on high marsh sites at North Inlet, South Carolina. The observed data have a slope of 31 $g \cdot m^{-2} \cdot yr^{-1}$ ($P < 0.0001$). Post-1999 projections are based on the sea-level rise scenario shown in panel C. (B) Predicted (dashed line) and observed (open circles) elevations in high marsh control sites (same controls as in Fig. 4A) relative to the time-zero (1996) elevation. (C) Observed (open circles) and projected (dashed line) summer (July and August) mean sea level in Charleston Harbor (relative to the 1984 level). The projection assumes that the 2000–2025 rate of increase in sea level continues at the current long-term 0.34 cm/yr rate.

and Fig. 6A). The model predicted this long-term trend (Fig. 6A), accounting for 44% of the variation in annual production, and predicted a 4.7 cm rise in marsh elevation over the next 25 yr (Fig. 6B) corresponding to a 6.8 cm rise in MSL (Fig. 6C).

The variability in primary production is in part due to the time lag between changes in mean sea level and adjustment in elevation of the marsh surface. Past mean

sea level in Charleston, South Carolina, displays several long-period cycles (Fig. 1) that have been used to forecast the low frequency sea-level variability for the period 2000–2025 (Fig. 6C). These sea-level cycles will in all probability have a significant effect on the productivity of the salt marsh (Fig. 6A). The resulting cycle of aboveground productivity is predicted to have a range of ~265 $g \cdot m^{-2} \cdot yr^{-1}$, which amounts to 37% of the mean annual production between 1984 and 1999 and, thus, is likely to be ecologically significant.

The long-period sea-level cycles include a prominent one of 28 yr in length (Fig. 1) that is not astronomically forced. In addition, several of the lunar constituents are modulated by an 18.61-yr cycle due to the regression of the nodes (Pugh 1987). The most significant modulation of tidal height in Charleston is due to M_2 with $f = 1.037$. As a result, the M_2 amplitude varies sinusoidally on an 18.61-yr cycle with the high tide 3.7% (or 5.5 cm) higher in Charleston than the mean at times of minimum lunar declination (18°18′), which occurred/occurs in July 1978, March 1997, October 2015, and May 2034 (Pugh 1987). Although the mean sea level is barely affected by the nodal period, other constituents besides M_2 also have modulated amplitudes and phases, including O_1 ($f = 1.187$), K_1 ($f = 1.115$), 2N2 ($f = 1.037$), μ_2 ($f = 1.037$), N_2, ($f = 1.037$) ν_2 ($f = 1.037$). The most significant nodal amplitude modulation in Charleston besides M_2 is due to O_1, with high tides exceeding the mean by 1.4 cm every 18.61 yr but maximized in November 1987, June 2006, and January 2024, when the moon is at its maximum declination (28°36′) (Pugh 1987). Although the mean sea level is apparently not affected by the regression of the nodes, maximum sea level will vary significantly during a nodal cycle and thus have additional effects on marsh production and sedimentation because of an associated ~7% change in tidal range.

Long-term changes in the mean sea level, and probably its range, affect primary productivity (Fig. 5A) because productivity depends on the relative elevation of the marsh surface (Fig. 2 and Eq. 2), which is a function of RSLR (Eq. 4). Moreover, there is an optimum rate of RSLR with respect to productivity. However, the optimum rate of RSLR, which in North Inlet was predicted to be ~1.2 cm/yr, is also close to the stable limit (Fig. 5A) where a further increase in RSLR or a positive sea-level anomaly will put the marsh surface below the lower limit of the growth range of *S. alterniflora*. The threshold RSLR should be lower in coastal wetlands that are deprived of sediment (low q value, Fig. 5). This is the situation for much of Louisiana's coastal wetlands where eustatic sea-level rise, rapid subsidence, and an anthropogenically reduced sediment supply combine to produce a rate of RSLR of ~1.0 cm/yr (Penland and Ramsey 1990), reduced productivity of wetland vegetation (Day and Templet 1989), and large-scale losses of coastal wetlands (Day and Templet 1989, Britsch and Dunbar 1993).

Conclusions

Primary productivity of salt marsh vegetation is regulated by changes in sea level, and the vegetation, in turn, constantly modifies the elevation of its habitat toward an equilibrium with sea level. The model described here explains the mechanics of how these communities modify their environment and how coastal wetlands remain stable against variations in sea level, and the conditions that lead to instability. Mean sea level is a moving target, and tidal marshes are constantly adjusting toward a new equilibrium.

An important conclusion of this study is the theoretical result that for every marsh there is an optimum rate of relative sea-level rise (RSLR), an optimum depth at which the marsh community is most productive, and an equilibrium depth that can be greater or less than the optimum (Fig. 5). These optima will vary regionally with differences in sediment and nutrient loading, tidal range, vegetation, and climate. These differences will give rise to a family of equilibrium response curves. For instance, it is both intuitive and predictable that salt marshes in regions like the southeast United States, where sediment loads are high (high q value), should be stable against a broader range of RSLR than those in sediment-poor estuaries, like those in the northeast United States (e.g., Fig. 5). It should be noted that differences in regional subsidence rates are already accounted for in the local value of RSLR and will not affect the optimum depth, but they will affect the equilibrium depth in so far as RSLR differs regionally due to subsidence.

We predict that the near-term stability of salt marshes in response to rising sea level depends on the present elevation of the marsh community in relation to its depth-response curve (Fig. 2) and the local mean sea level (MSL). The current equilibrium depth in regions of high RSLR could be superoptimal (suboptimal elevation) for the marsh vegetation, which would be evidence for an unstable and deteriorating marsh community where even high rates of primary production would not necessarily ensure marsh stability. Conversely, marsh communities situated at less than optimum depths are predicted to be stable against variations in MSL (Fig. 5). Our findings indicate that in areas of meso-tidal range and high sediment loadings, coastal wetlands could be stable against a RSLR as great as ~1.2 cm/yr, assuming a monotonic rise in MSL. However, MSL displays a number of long-period cycles and interannual variability (Fig. 1) which, when superimposed on a long-term rate of 1.2 cm/yr, would exceed the limit during ascending phases of the cycle. In conclusion, our model demonstrates the counterintuitive result that a salt marsh at its maximum productivity (i.e., at its optimum elevation and rate of RSLR) is not the most stable. Rather, a less productive marsh situated above its optimum elevation should be more stable because it will tolerate a higher RSLR and is less vulnerable to the variability in MSL.

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